# LARVAL DEVELOPMENT IN BLISTER BEETLES OF THE
## GENUS *LINSLEYA* (COLEOPTERA: MELOIDAE)

RICHARD B. SELANDER

Departments of Genetics and Development and of Entomology, University of Illinois, Urbana, Illinois 61801.

*Abstract.*—Twenty $T_1$ larvae of *Linsleya convexa* (LeConte) failed to feed on pollen taken from the comb of the honeybee. Two of nine $T_1$ larvae given eggs of the acridid grasshopper *Melanoplus differentialis* (Thomas) completed the developmental pattern $T_1$-$FG_{2-5}$-$C_6$ in 23 and 27 days. After being chilled at 5°C for two months to break diapause, one of the larvae reached instars $SG_7$, $P_8$, and $A_9$ in 19, 24, and 34 days, respectively. The other larva molted to instar $C_7$ after chilling but failed to complete ecdysis.

A previous contention that *L. sphaericollis* (Say) regularly follows the abbreviated ontogenetic pattern $T_1$-$FG_{2-5}$-$P_6$-$A_7$, with diapause in instar $FG_5$, is regarded as unfounded.

Some anatomical features of the larva and pupa of *L. convexa* are described. It is concluded that, while *Linsleya* does not belong in the Lyttina, the evidence for placing it in the Epicautina is, as a whole, equivocal.

Following MacSwain's (1951) proposal, based on external anatomy of the first-instar (triungulin) larva, that the genus *Linsleya* MacSwain be assigned to the subtribe Epicautina, rather than the Lyttina, several workers have addressed the question of whether species of this genus are, like most species of the genus *Epicauta* Dejean, predators of the eggs of acridid grasshoppers (Selander, 1964; Selander and Pinto, 1967; Church and Gerber, 1977). The question is certainly an important one systematically, since an affirmative answer would provide strong support for MacSwain's hypothesis.

Selander (1964) called attention to a report of Criddle (1931), in which *Linslelya sphaericollis* (Say) was cited as one of several "enemies" of grasshoppers in Canada, and of Romanov (1954), in which the larva of this species was stated to be predaceous on grasshopper eggs in Manitoba. Unfortunately, neither report gives any indication whatsoever regarding the evidence for the reputed predation of grasshopper eggs by larvae of *L. sphaericollis*. On the other hand, Church and Gerber (1977) reported that "none

of several hundred meloids" taken from egg pods of *Melanoplus sanguinea* (Fabricius), *M. bivittatus* (Say), and *Camnula pellucida* Scudder in the Canadian prairies "in recent years" proved to represent *Linsleya sphaericollis*, even in instances where adults of this species were abundant in the area in which grasshopper eggs were collected. Moreover, Selander and Pinto (1967) reported failure of 24 larvae of *Linsleya convexa* (LeConte) to feed on eggs of *Melanoplus differentialis* (Thomas) in an attempted laboratory rearing.

At this point one might suspect that the reports of Criddle and Romanov were perhaps suppositional and that grasshopper eggs are not, in fact, the prey-type of larvae of *Linslelya*. Yet Church and Gerber (1977) and Peterson (cited by them) were able to induce a small percentage of larvae of *Linsleya sphaericollis* to feed on the eggs of *Melanoplus* in the laboratory and in one instance actually obtained a complete rearing to the adult stage.

In this article I report an experimental rearing of *Linsleya convexa* in which first-instar larvae were given, as prospective food, either pollen provisioned by the honeybee (*Apis mellifera* Linnaeus) or eggs of the grasshopper *Melanoplus differentialis*. In addition, I describe some of the anatomical features of the larva and pupa of *L. convexa*.

## An Experimental Rearing *Linsleya convexa*

Materials and methods.—I follow Selander and Mathieu (1964) in referring to the four phases of the larval stage of Meloidae as triungulin, first grub, coarctate, and second grub, commonly denoted by the symbols T, FG, C, and SG, respectively, with numerical subscripts to indicate instar, as necessary.

The experiment utilized 29 T larvae of *Linsleya convexa* eclosing from an egg mass laid by a female that was part of a group of adults collected at Fort Davis, Jeff Davis County, Texas, 3/10 August 1968, on *Chilopsis linearis* and *Tetraclea coulteri*. The eggs, laid 13 August at the collection site, were placed in a 3-dram vial and held at ambient temperature, 100% RH, in darkness until 15 August, when temperature was stabilized at 27°C. The egg mass contained 30 eggs, all of which hatched on 5 September (24 days). Larvae remained under the conditions of incubation before use in the experiment.

Twenty larvae were given pollen at the age of seven days (12 September); nine were given grasshopper eggs at the age of 10 days (15 September). One larva from the lot died at the age of 8 or 9 days, before entering the experiment.

Pollen was removed from a comb of the honeybee shortly before use, mixed with distilled water, and worked into small balls, as described by Selander and Mathieu (1964). The amount of water was varied to produce

five balls each of four consistencies (from "rather dry" to "soupy"). Each ball was placed on the inner surface of a cotton-plugged glass tube (4 mm inner diameter), and a *Linsleya* larva was deposited on one of the cotton plugs near the pollen ball.

*Melanoplus differentialis* eggs were nine months old. They had been incubated initially at 27°C, 100% RH for 1–2 months in order to allow them to develop to the diapause state and then held at 5°C until use. Larvae of *Linsleya* were given about 40 *Melanoplus* eggs each in individual cotton-plugged glass tubes 8 mm inner diameter. Allotments were random selections of eggs from 50 egg pods.

Larvae receiving pollen were placed at 27°C, 100% RH, in darkness. Those receiving *Melanoplus* eggs were placed initially under the same conditions, but on day 8, surviving, unfed larvae were transferred to 35°C. Larvae that completed feeding in instar $FG_5$ were transferred to a sand/soil mixture (moistened with 10% water by volume). Subsequent treatment of larvae is described in the section on results.

Results.—All 20 larvae of *Linsleya convexa* given pollen died in the T phase, evidently without feeding. Seventeen became mired in the pollen and apparently drowned on day 1; two did so on day 2. On day 3 the lone survivor was transferred to a larger tube (8 mm inner diameter) with a fresh pollen ball of medium consistency in which a small amount of honey had been incorporated. This larva survived 31 days in rearing. The length of the survival period might be interpreted as evidence that the larva was obtaining some nourishment from the pollen ball. However, some of the T larvae of *L. convexa* studied by Selander and Pinto (1967) lived as long as 23 days at 27°C without feeding, and some of those of *L. sphaericollis* studied by Church and Gerber (1977) survived without food for 4–7 weeks on moist soil at 20°C.

Seven of the nine larvae of *L. convexa* given *Melanoplus* eggs died in the T phase, without feeding, in a mean of 13.1 (1.78) days (range 8–22). One larvae (#1, a female), after transfer to 35°C, began feeding on an egg on day 10; reached instars $FG_2$, $FG_3$, $FG_4$, and $FG_5$ on days 11, 13, 15, and 17, respectively; was transferred to sand/soil on day 22; and ecdysed to $C_6$ on day 27. A day later it was returned to 27°C. Another larva (#2, a male), which remained at 27°C, began feeding on day 2; reached instars $FG_2$, $FG_3$, $FG_4$, and $FG_5$ on days 5, 7, 9, and 12, respectively; was transferred to sand/soil on day 17; and ecdysed to instar $C_6$ on day 23.

In the FG phase both larvae produced a feces of paste-like consistency which was spread over the grasshopper eggs and on the sides of the glass tubes as droplets. In $FG_5$ both larvae excavated a cell in the sand/soil in which they became motionless two days before ecdysis occurred.

On day 176 of the experiment the two C larvae, which were evidently in

diapause, were transferred to 8 mm inner diameter tubes and placed at 15°C, 100% RH, in darkness. After 60 days they were returned to 27°C, again at 100% RH in darkness.

Larva #1 broke diapause and entered instar $SG_7$ 19 days after chilling ended (day 255), pupated five days later (day 260), and reached the adult stage 10 days after that (day 271). The adult was perfectly formed and of exceptionally large size (length, to end of elytra, 15 mm; cf. Selander, 1955). Larva #2 was killed 871 days after chilling ended (day 1107), at which time I found that it had molted, at some time during the post-chilling period, to instar $C_7$ inside the $C_6$ skin. The occurrence of two consecutive instars in the coarctate larval phase was recorded previously in *Pyrota palpalis* Champion by Selander and Mathieu (1964).

Discussion.—The results of the experiment are consistent with the rearing attempts of Church and Gerber (1977) in two major respects. First, it is now established that the larva of *Linsleya convexa*, like that of *L. sphaericollis*, is capable of developing to the adult stage on a diet of the eggs of *Melanoplus* grasshoppers. Second, as in the case of *Linsleya sphaericollis*, only a small proportion of *L. convexa* larvae provided with *Melanoplus* eggs in the laboratory respond positively to them.

In Church and Gerber's (1977) rearing of *Linsleya sphaericollis* on the eggs of *Melanoplus sanguinipes* and *M. bivittatus*, 16(4.3%) of 370 T larvae fed, 12 (3.2%) reached $FG_2$, and 8 (2.2%) reached $FG_5$. Five of the $FG_5$ larvae "lived 4 to 10 weeks at 20°C after they stopped feeding, but remained unchanged"; the fate of the remaining three was not mentioned. Peterson, in an unpublished study cited by Church and Gerber, obtained 31 FG larvae from 240 T larvae given food (12.9%); the percentage of success might have been higher had he reared each of the larvae individually, rather than placing 1–5 in a vial. Two of the FG larvae lived until at least day 76 of his rearing. In addition, a dead adult was found on day 76 among material kept at 29°C, having "evidently pupated directly from the fifth instar [$FG_5$]" (Church and Gerber, 1977).

A possible explanation for the poor feeding response obtained in the laboratory for both species of *Linsleya* is suggested by the exceptionally long survival period of T larvae under starvation, mentioned above. Comparable longevity is charactersitic of T larvae of *Epicauta pennsylvanica* (DeGeer) from Illinois and Mississippi (Selander, unpublished data). Moreover, larvae of this species, like those of *Linsleya*, are very unlikely to feed in the first few weeks following eclosion. In this case it can be shown that the newly eclosed T larvae are in a behavioral diapause state. A procedure that I have found effective in rearings of *E. pennsylvanica* is to chill newly eclosed T larvae for two months at 5°C. It might be interesting to see the effect of this or a similar treatment on the feeding response of T larvae of *Linsleya*.

Church and Gerber (1977) concluded that their and Peterson's FG₅ larvae of *Linsleya sphaericollis* that survived for several weeks were in diapause when they died and that "hypnothecal" (C) and "non-vorant" (SG) phases of the larval stage "probably seldom or never occur in this species." Further, they speculated that in nature larvae overwinter in instar FG₅, pupate directly from that instar in spring, and emerge as adults a few weeks later. Not only that, since the FG₅ larvae are "much less resistant to desiccation than [coarctate larvae] and likely could not survive more than one winter, a 1-year life cycle is indicated"!

This is highly imaginative ecology and, for all I know, may be true. But on the basis of the actual evidence, it is hardly to be taken seriously. The failure of the larvae of *L. sphaericollis* to develop beyond the FG phase may have been simply the result of lack of access to soil of proper moisture content (whether any soil was available to them in Church and Gerber's rearing is not stated). Although some Lyttini can complete the FG phase without access to moist soil, in my experience it is an absolute necessity for species of *Epicauta*. Nor can the possibility of disease or nutritional inadequacy of the food be ruled out. But in any event, arrested development is, by itself, hardly proof of diapause, especially when it terminates in death.

If, as Church and Gerber report, Peterson's adult did not pass through the C phase of larval development, this in itself may be taken as good evidence for regarding *Linsleya* as an epicautine genus, since the abbreviated pattern T-FG-P-A has been recorded previously only in members of the genus *Epicauta* (Selander and Weddle, 1969). However, no species of the subfamily Meloinae is known to diapause in the FG larval phase and no species of Meloidae is known to follow only the abbreviated ontogenetic pattern, and it was at best ingenuous, considering the fragmentary nature of their information, for Church and Gerber to suggest that *Linsleya sphaericollis* does so.

## Anatomy

The triungulin (T₁) larva of *Linsleya convexa* was described and illustrated by MacSwain (1956). Some anatomical features of the FG₂, FG₅, C₆, and SG₇ larva and of the pupa are noted below. The descriptions are limited to characters which, in my experience, vary significantly among genera and other higher taxa of Meloidae. Except in the case of the C₆ larva, they are based on exuvia.

FG₂ larva.—Cuticle sparsely but conspicuously clothed throughout with relatively long, slender setae. Spiracles lateral. Labrum rectangular, with anterior margin straight and with 8 setae in median transverse row. Mandible (Fig. 1a) with a series of 9–10 vestigial, blunt teeth on mesodorsal margin, terminating basad in a large, prominent, triangular tooth; mandibular setae
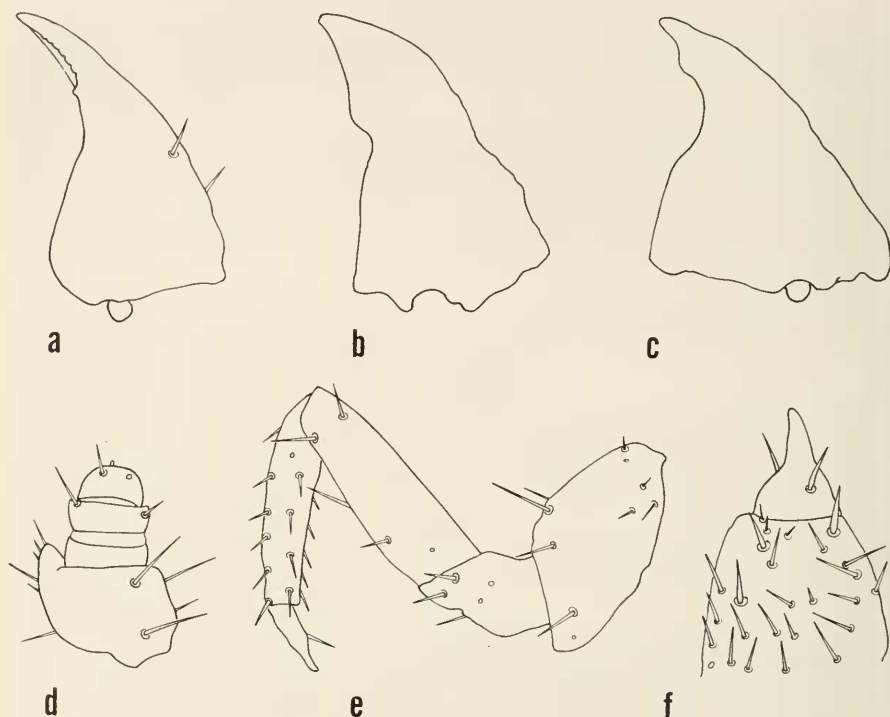
Fig. 1. *Linsleya convexa.* a, Right mandible of $FG_2$ larva, dorsal view. b, Right mandible of $FG_5$ larva, dorsal view. c, Right mandible of $SG_7$ larva, dorsal view. d, Left maxilla of $FG_2$ larva, ventral view. e, Right leg II of $FG_2$ larva, anterior view. f, Tibia and tarsungulus III of $FG_5$ larva, anterior view.

equal in length. Antennal segment III about $3/10$ as long as II, with terminal seta $2^1/3 \times$ as long as III; II bent, with sensory appendix rounded, button-like, lateral. Maxilla (Fig. 1d) with mala prominent, glabrous ventrally, with several setae dorsally; palpus retaining orbicular form much as in $T_1$. Labial palpus with segment II tapered, as long as I. End of abdomen with a row of 4 long setae of equal length. Leg (Fig. 1e) elongate, rather heavy, with a definite pattern of setation; coxa prominent; tibia about $1^1/5 \times$ as long as femur; tarsungulus $1/4$ as long as tibia, bearing a single seta.

$FG_5$ larva.—Cuticle relatively densely, very conspicuously clothed with setae, most of which are heavy and rather short. Mandible (Fig. 1b) much more massive than in $FG_2$, lacking teeth. Antennal segment III less than $1/4$ as long as II, less than $1/3$ as wide, with terminal seta about as long as III; II $3/5$ as wide as long, with sensory appendix terminal, slightly wider than III. Maxilla with mala massive, sparsely setate ventrally, densely so dorsally;
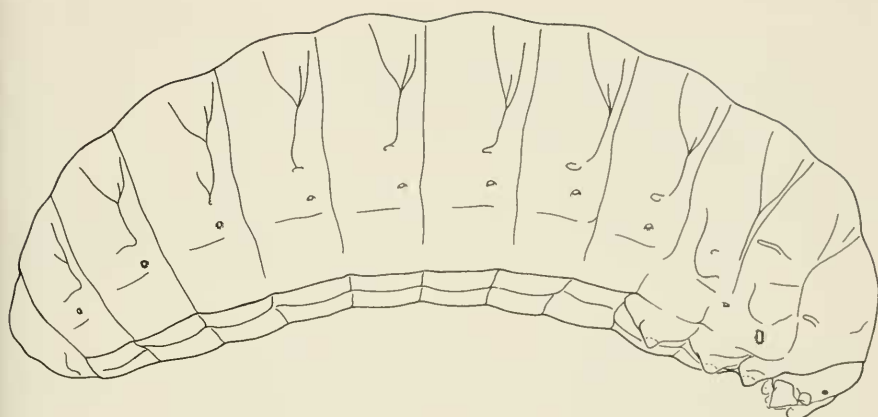
Fig. 2.    C$_6$ larva of *Linsleya convexa*.

palpus not so orbicular as in FG$_2$. Labial palpus less elongate than in FG$_2$. Leg (Fig. 1f) heavy, relatively short, densely setate; tarsungulus well developed, bearing 2 setae.

C$_6$ larva (Fig. 2).—Subnavicular, slightly curved, lacking lateral ridge on abdomen. Cuticle uniform light brown in color, uniformly pebbled, completely lacking striae. Mandible stubs acute. Spiracular cones small, not at all bulbous or sagged posteriad; spiracular openings very small. Dorsal line of dehiscence well developed and complete on thoracic segments and abdominal segments I–VI.

SG$_7$.—Similar to FG$_5$. Mandible (Fig. 1c) much wider, with a chisel-like flange on mesal margin. Antenna, maxillary palpus, and labial palpus somewhat shorter; antennal segment III flattened, at least in exuvia hardly distinguishable as a separate segment. Leg lacking tarsungulus.

Pupa (P$_8$).—Propping spines conspicuous, each with a spinelike seta at apex; 4 small spines on head; 10 (6 very large) on pronotum; none on meso- and metathorax; 4 (2 large) on abdominal segment I, 6 on II–VII, 4 (small) on VIII.

Remarks.—With respect to the conspicuous setation of the body and the leg structure in FG$_2$ and the distribution of propping spines in the pupa (absent on mesothorax, few in number and strictly dorsal on abdomen), *Linsleya convexa* is more epicautine than lyttine. However, it differs strikingly from *Epicauta*, and at the same time agrees with the Lyttina and Pyrotina, in most of the characters of the coarctate larva mentioned above.

In view of the paucity of published work on the comparative anatomy of immature meloids other than the triungulin larva, it is difficult to interpret the curious mixture of lyttine and non-lyttine characteristics found in *Lin-*

*sleya*. It is, however, apparent that there is little about the genus that is specifically epicautine. Since grasshoppers eggs are the typical prey-type of larval Mylabrina (MacSwain, 1956), as well as of *Epicauta*, even positive proof that *Linsleya* utilizes this prey-type in nature would not constitute definitive evidence that the genus is epicautine. Pinto (1974) claimed to find special similarity in patterns of courtship of *Linsleya* and *Epicauta*, but his treatment was based on a decidedly restricted survey of the range of behavioral variation in the tribe Lyttini, and I fail to find his argument convincing. Indeed, it would appear that the only unequivocal basis for including *Linsleya* in the Epicautina is the characteristic originally cited by MacSwain (1951): the presence of lanceolate setae on the legs of the T larva. An alternative interpretation, and one apparently not considered heretofore, would be to place *Linsleya* in a separate subtribe, allied to the Epicautina and Mylabrina, at least phenetically, on bionomic grounds.

## Literature Cited

Church, N. S. and G. H. Gerber. 1977. The development and habits of *Linsleya sphaericollis* (Coleoptera: Meloidae). Can. Entomol. 109: 375–380.

Criddle, N. 1931. Grasshopper control in Canada east of the Rocky Mountains. Can. Dep. Agric. Bull. 143(n.s.), 18 pp.

MacSwain, J. W. 1951. A new genus of Meloidae from North America. Pan-Pac. Entomol. 27: 58.

———. 1956. A classification of the first instar larvae of the Meloidae (Coleoptera). Univ. Calif. Publ. Entomol. 12, 182 pp.

Pinto, J. D. 1974. Courtship behavior in *Linsleya compressicornis* and its taxonomic significance (Coleoptera: Meloidae). Pan-Pac. Entomol. 50: 1–8.

Romanov, W. 1954. Predators of grasshoppers. Proc. Entomol. Soc. Manit. 9: 14–18.

Selander, R. B. 1955. The blister beetles genus *Linsleya* (Coleoptera, Meloidae). Am. Mus. Novit. 1730, 30 pp.

———. 1964. The systematic position of the genus *Linsleya* (Coleoptera: Meloidae). Proc. Entomol. Soc. Wash. 66: 216.

Selander, R. B. and J. M. Mathieu. 1964. The ontogeny of blister beetles (Coleoptera, Meloidae). I. A study of three species of the genus *Pyrota*. Ann. Entomol. Soc. Am. 57: 711–732.

Selander, R. B. and J. D. Pinto. 1967. Sexual behavior in blister beetles (Coleoptera: Meloidae) II. *Linsleya convexa*. J. Kans. Entomol. Soc. 40: 396–412.

Selander, R. B. and R. C. Weddle. 1969. The ontogeny of blister beetles (Coleoptera, Meloidae). II. The effects of age of trungulin larvae at feeding and temperature on development in *Epicauta segmenta*. Ann. Entomol. Soc. Am. 62: 27–39.